SECONDARY PRODUCTIVITY OF TERRESTRIAL ECOSYSTEMS
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WARSZAWA 1967 KRAKÓW

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3. 2. 4 Investigation on heterotrophic productivity in forest insect communities*

1. INTRODUCTION

Measurement of heterotrophic productivity in insect communities presents a challenge because of the variety of species and host plant associations combined with the potential for rapid turnover of biomass. In the forest canopy this complexity is compounded by inaccessibility to the customary collecting and sampling techniques for both insect populations and their plant hosts. These difficulties account in part for the dearth of published information on productivity in forest canopy insect communities. Some of the available information on forest insect populations includes such pertinent facets as food consumption and utilization, population growth rates, and losses to predation or parasitism. But to interpret this information in terms of secondary production requires knowledge of other aspects of energetics in the particular ecosystem involved. At a minimum, the broad outlines of total energy flow through the ecosystem must be specified as a context for data on production by insects. Often the acquisition of such broad numbers transcends the scope of the original research.

The investigations reported here have attempted to overcome some of the difficulties by employing a multi-disciplinary approach and by use of radioisotope techniques. The forest stand under study consists of a small

* Research sponsored by the U. S. Atomic Energy Commission under contract with the Union Carbide Corporation.

(500 m^2) area of rich *Liriodendron* forest which is under simultaneous investigation by workers representing a variety of scietific disciplines. The central research theme for the project is elucidation of cesium-137 movement through the ecosystem, with objectives of measuring rates of cycling, determination of standing radiocesium distribution and transfer rates in food chains and other components, and derivation of information for predicting the behavior of this hazardous radionuclide in entire landscapes (Auerbach, Olson, Waller 1964). Most (30) of the *Liriodendron* trees in the stand were tagged by trunk inoculation with cesium-137 in May 1962, and subsequent studies have followed the movement of radioactivity within trees and transfer to litter and soil layers (Olson 1965), within litter, soil, and microorganism components (Witkamp and Frank 1964), through forest floor food chains (Reichle and Crossley 1965), and in further work now under way.

In some instances information on radioisotope movement among the components of the forest ecosystem provides data difficult to obtain by more conventional means. Radiotracers have been utilized in studies of the decomposition of leaf litter (Olson and Crossley 1963) and the role of arthropods and microflora in the breakdown of leaf litter (Crossley and Witkamp 1964, Witkamp 1966). Radioactive food bases have yielded valuable information on arthropod-plant relationships (Crossley and Howden 1961, Paris 1965), and offer a technique for the measurement of arthropod food consumption, metabolism and energy flow in natural ecological systems (Hubbel, Sikora, Paris 1965, Crossley 1966, Reichle 1967). In the arthropod aspects of the tagged forest study, we are attempting to combine tracer techniques with more conventional ecological methods for analyses of energy flow in forest arthropod food chains, including canopy areas, litter arthropods, and soil microarthropods.

This report emphasizes the utilization of radioactive tracers to obtain information on heterotrophic production. Much of our data are preliminary but their inclusion seems worthwhile because so little is presently available on production by canopy insects.

2. MATERIALS AND METHODS

2.1 FOREST STUDY AREA

The forest study site is a second-growth tulip poplar stand located within the U. S. Atomic Energy Commission Reservation at Oak Ridge, Tennessee. The experimental area is one of a series of sinkholes in an isolated part of the Reservation, exhibiting a mesophytic flora characteristic of fertile sites in the Southern Appalachian Region. The forest is dominated by tulip poplar

(*Liriodendron tulipifera* L.) and includes short-leaf pine (*Pinus echinata* Mill.), red oak (*Quercus rubra* L.), and red maple (*Acer rubrum* L.). The understory is composed of dogwood (*Cornus florida* L.), redbud (*Cercis canadensis* L.) and saplings of canopy species. The major herbaceous species are the woody hydrangea (*Hydrangea arborescens* L.), Virginia creeper (*Parthenocissus quinquefolia* (L.) Planch.) and the Christmas fern (*Polystichum acrostichoides* (Michx.) Schott). The effective growing season extends from mid-April to late September.

The oldest trees in the forest stand are about 45 years. The average crown height is about 75 ft to 40 ft (23 to 12 meters) where the understory species predominate. To facilitate foliage and insect sampling in the lower canopy levels and understory, a 42-ft (13-meter) five-level tower was constructed in the middle of the stand. For more extensive sampling in upper canopy levels a boom truck with a 65-ft (20-meter) reach has been employed (Fig. 1).

In May 1962, a 500 m^2 portion of this forest ecosystem was tagged (Auerbach, Olson, Waller 1964) with cesium-137, a biologically mobile isotope with a physical half-life of about 30 years. Thirty-five trees within the experimental area were inoculated with a total of 467 mc of ^{137}Cs in doses ranging from 0.4 mc to 94.2 mc using a DBH power function formula to calculate a quantity of isotope per tree approximately proportional to tree mass.

2.2 SAMPLING AND ANALYTICAL PROCEDURES

Because of the small size of the stand and the smaller fraction of the canopy available for insect sampling, procedures were adopted which involved a minimum of destructive sampling. Most of the estimates of insect numbers and radiocesium content are based on collections and observations from four trees accessible from the 42-ft tower, supplemented by collections from peripheral trees obtained with ladder or lift trucks (Fig. 1). Populations of nonflying arthropods (including immature stages) were assayed two or three times per week (June through August) by enumerating them on 300-odd leaves which could be reached from the tower. Individual branches were marked and coded so that those used for population enumeration were distinguished from those sampled for radioactivity. The resulting data (insects per leaf) were transformed to biomass estimates by using the mean number of *Liriodendron* leaves per m^2 (Olson, personal communication). The same enumeration procedure was used for adult insects; those actually in flight were not included. Periodically, arthropods were collected for radioanalysis together with leaves or with 20-mm^2 discs punched from the leaves as discussed below, so that radiocesium content of the arthropods could be related to concentrations in the branches from which they were collected. Frequency of collection depended upon abundances and availability of the various species.

Insects were killed immediately upon collection to prevent biological elimination of radiocesium.

Radiocesium content of plant materials and larger insects was assayed with a Packard Instrument Company 410A Auto-Gamma Spectrometer. For smaller insects such as ants and aphids better results were obtained with a Johnson Laboratories E-150 Count Beta detector, a gas-flow proportional detector which analyzed the beta emissions of ^{137}Cs.

2.3 RADIOISOTOPE TRACER METHODS

Techniques for utilizing radioisotopes in the study of food chains have developed rapidly in the last few years (e.g., Odum and Kuenzler 1963, Hubbell, Sikora, Paris 1965, Reichle and Crossley 1965, Crossley 1966).

The principal applications have been in detection and delineation of food chains, quantification of food consumption, metabolic measurements in natural populations, and studies of local migrations. All of these applications are involved to some degree in our study, but the measurement of food consumption has received most emphasis. Both field and laboratory data are needed, since the methods basically consist of acquiring information on the distribution of radioactive tracer along a food chain after the equilibration processes have occurred, and interpreting these with rate functions obtained from laboratory work.

The rate of biological elimination for a radioisotope usually is expressed as a biological half-life (T_b), i.e., the time required to eliminate 50 percent of an ingested dose of radioisotope. For most insect species biological half-lives for cesium are relatively short, usually one or two days or less. In laboratory studies, test insects were fed tracer amounts of radiocesium and then were counted for radioactivity at intervals of several hours. For larger forms, such as geometrid larvae, individual insects were counted through time. In studies on aphids the experimental unit was a colony on a seedling plant which could be placed inside a Packard Instrument Company ARMAC small-animal detector. Biological half-lives (T_b) were estimated from these measurements of radiocesium retention either graphically or by means of a least-squares regression equation of log radiocesium content on time.

In the tagged forest area, insects feeding on plants accumulate ^{137}Cs until a steady-state equilibrium is reached. Then there is no further change in ^{137}Cs concentration in insects, since intake (through consumption of plants) is balanced by loss (through biological elimination). This balance is given by:

$$I = kQ$$

where I is intake of radioactive cesium in food, Q is the ^{137}Cs in the insects' and k is the elimination coefficient which is numerically equal to $0.693/T_b$.

The product kQ thus represents the amount of turnover of radiocesium per unit time. In application, steady-state values (radiocesium concentrations) were measured for *Liriodendron* leaves, and sap, and for the associated herbivorous and predaceous arthropod species. Laboratory values for biological half-lives gave an estimate of the elimination coefficient, k. The product kQ was then an estimate of I, the intake of radiocesium. Since the ^{137}Cs concentration in the food was also measured, mean intake could be expressed in terms of weight food consumed per unit time. Calorimetric conversions, finally, expressed consumption in terms of energy.

Several methodological refinements are necessary and will be explained in the text. While biological half-lives could not be measured for each insect species, a function was developed relating biological half-life to size of insect, so that turnover times could be predicted from size. Also, laboratory measurements were made under controlled temperature conditions, and in application to field data corrected to field temperatures using a Q_{10} relationship.

3. RESULTS

3.1 RADIOCESIUM TURNOVER BY INSECT SPECIES

Biological half-lives for radiocesium have been reported for a variety of insect species (see Crossley 1966). Laboratory studies on radiocesium elimination by two insect species important in the forest canopy will be given here. A relationship between insect body size and cesium retention previously reported (Crossley 1963a) is further developed for estimating biological half-lives and treating mixed species populations of insects. Factors influencing the rate of radiocesium turnover are also considered, including the effects of environmental temperature, metabolism, and the production of young.

Fig. 2 shows the retention of ^{137}Cs by geometrid caterpillars collected from tagged *Liriodendron* trees. These insects were brought into the laboratory and maintained on uncontaminated food while the rate of ^{137}Cs loss was being measured. Data indicate a biological half-life of about 27 hrs at 15° C and 13 hrs at 24° C, with the elimination rate doubled for a 10° C rise in temperature. These and other experiments suggest that the rate of bioelimination is a function of the general metabolic rate of the insect (Reichle 1967). Within the range of temperatures at which these insects are active the correlation of temperature and biological half-life follows the Q_{10} rule of Van't Hoff, with a value of approximately 2 for the Q_{10} relationship.

At present radiocesium uptake and turnover are being studied in laboratory work on the Liriodendron aphid, *Macrosiphum liriodendroni* Monell. Laboratory studies have been completed for the common bean aphid, *Aphis fabae* Scop., which probably has a metabolism similar to that of *Macrosiphum* as regards cesium turnover times. Fig. 3 shows retention of cesium-134 by groups of

aphids (*Aphis fabae*) maintained at three temperatures, and for which production of young was treated differently. In these experiments the groups of aphids were counted for radioactivity *in toto* by placing the entire plant seedling within a detection chamber. The upper part of Fig. 3 illustrates data obtained when newly born aphids were left in place with their mothers on the seedling during the experiment. Decrease in radioactivity then represents only biological elimination (metabolic turnover) of the radioisotope from the aphids. Since newly-born aphids were left on the seedling, their radioactivity continued to be detectable. In other experiments (lower part of Fig. 3) young aphids were removed prior to counting for radioactivity, so that loss rates represent metabolic turnover of radiocesium plus transfer from mother to young. In this way the decreasing radioactivity reflects losses due to both bioelimination and natality. Metabolic turnover measured separately showed approximately a doubling of elimination rate with 10° increase in temperature (top of Fig. 3) over the range 8° to 28°. Bioelimination plus production yielded rates which more than doubled for a 10° increase in temperature. At 8° C biological half-lives were similar in the two experiments (43 hr vs 45 hr) and production of young was negligible (only 9 per 30 adults). At higher temperatures significant reproduction resulted in more rapid turnover (14 vs 21 hr at 18°, 7 vs 9 hr at 28°). In these experiments some excreta (in the form of honeydew) accumulated on the leaves of the plant so that, by the time radiocesium retention in aphids had dropped to about 20 percent of the initial amount, radioactivity from the contaminated plants interfered with attempts at further measurements. Currently, experimentation with *Macrosiphum liriodendroni* involves new procedures for radioactivity detection in individual aphids removed from seedlings.

It would not be practical to measure biological half-lives for each species in the insect community. Fortunately the elimination rates are proportional to the size of the insect (in the case of radioisotopes of cesium, at least) so that biological half-lives can be predicted for insects from their sizes (Crossley 1963a). The biological half-lives (at 20° C) of radiocesium in seven herbivorous insect species are presented in Fig. 4 as a function of the fresh weight (mg) of the insect. All values are based on adults except for the two lepidopterans (*Thyridopteryx ephemeraeformis* (Haworth) and *Geometridae*) which were larvae. The largest insect examined *Romalea microptera* (Beauvais), a grasshopper species, had a live weight of about 5,000 mg, and the relationship appears to extend validly to animals as small as the beetle *Chrysomela knabi* Brown (23 mg). Biological half-lives for cesium in mammal species, as reported by Langham and Anderson (1959), would fall close to a projection of the line in Fig. 4. This relationship evidently does not hold for smaller insects (such as *Aphis fabae*) or perhaps for any suctorial insects; the hemipteran *Oncopeltus fasciatus* (Dallas) had a slower turnover of cesium than would have been predicted from its size alone (Crossley and Dodson 1965).

Size of insect species can thus be made the basis for estimation of cesium turnover rates from the relationship of Fig. 4, provided certain restrictions are applied. Since the rate of cesium elimination has been demonstrated to be a function of the general metabolic rate (Reichle 1967), there is a strong possibility that the size-T_b relationship actually represents a correlation with the general metabolic rate. This correlation could explain the deviation of extremely small insects from the relationship of Fig. 4. This line should only be used for species in the same general size category (10—10,000 mg) and likewise it should not be extended to species with different feeding patterns. The ecological position of species within the community also may be important in estimating the T_b for cesium. Decomposer arthropods on the forest floor have a body size-T_b relationship with a similar slope to that of Fig. 4, but the T_b's themselves are about an order of magnitude longer (Reichle and Crossley 1965). However, it can be demonstrated that the general metabolic rates of cryptozoan and herbivorous species are likewise dissimilar.

3.2 RADIOCESIUM DISTRIBUTION IN CANOPY FOOD CHAINS

Measurements in the summer of 1965 determined the steady-state concentrations of ^{137}Cs in foliage, its sap, and herbivorous and predaceous animals which comprise the insect community in the *Liriodendron* canopy. These equilibrium concentrations of radioisotope represent the standing distribution of radiocesium along the generalized food chain. They form the basic data for estimation of total radiotracer movement and, ultimately, movement of energy through the various trophic levels.

To estimate the ^{137}Cs content of canopy foliage, regression equations were developed to predict the total leaf radiocesium concentrations from analyses of subsamples using one, two, and three leaf punches per individual leaf. Results indicated that two punches per leaf were much better for estimation of entire leaf concentrations than was a single punch, although three punches gave no significant improvement. To minimize foliage destruction, the two-punch procedure was used for leaf assays. Removal of punches apparently did not alter the distribution of ^{137}Cs in the remaining leaf (Fig. 5*A*). Measurement of foliage concentrations of a given branch with 95% confidence limits within 10% of the mean would require sampling of at least 71 leaves with two punches removed from each.

In Table I are listed the mean ^{137}Cs leaf concentrations (pc/mg) (10^{-6} curies/mg) for branches examined during the study period. The regression equation used in calculating branch concentrations was

$$\hat{Y} = 41.65 + 0.4284X$$

where $\hat{Y}$ is the whole leaf (petiole plus blade) concentration and X is mean concentration in punches. Mean ^{137}Cs concentration in foliage on the branches

examined was 47.0 ± 2.59 pc/mg dry weight. Since cesium concentrations in insects collected during the summer were normalized to a percentage of leaf values, the data in Table I enable ^{137}Cs concentration factors in insects to be converted to actual activity levels (pc/mg) when desirable. Due to the individual branch differences, these data do not depict clearly the seasonal behavior of ^{137}Cs in the forest canopy. However, more extensive collections and repeated measurements on the same branches and trees have demonstrated a consistent pattern of ^{137}Cs distribution in foliage during successive growing seasons (Olson and Waller 1965). Maximum radiocesium levels occur in new leaves by early June; thereafter there is a slight but steady decrease in concentrations due to the dilution of the available cesium pool by additional growth and production of new leaves. Following the initial inoculum in 1962, canopy concentrations have dropped by a factor of 1/3 during each successive growing season, with the soil acting as a reservoir for cesium leached from decomposing leaves and transferred through the root mat.

In order to reference the ^{137}Cs concentrations of sap-feeding insects to their food base, radioanalyses were made of the cesium concentrations in petiole-sap exudates. Because of the small quantities of material obtained, and consequently low levels of radioactivity, the ^{137}Cs beta emissions were counted in a low-background gas flow proportional counting system (background ≃ 0.2 cpm). All samples were air dried before counting. Sap determinations were made on petiole samples from a single *Liriodendron* branch with high ^{137}Cs concentrations (71.9 ± 4.49 pc/mg dry wt of foliage). Sap values ran 362.9 ± 37.78 pc/mg dry wt, giving a concentration factor over foliage on a dry wt basis for sap of about five. There was greater variation within individual sap determinations than between whole leaf radiocesium levels. The relative variation between sap and leaf measurements, as expressed by their respective coefficients of variation, were 17.7% for leaves and 37.6% for sap. Greater variation appears to be inherent in subsamples of foliage constituents compared to average values for the entire leaf.

The phloem sap of *Liriodendron* consists mostly of a sucrose solution, with a specific gravity range of from 1.03 to 1.07 — 8 to 18% dry weight (Zimmermann, personal communication). Using a median value of 13% dry wt sucrose (137 mg sucrose/ml) yields the equivalence of one mg dry wt sap/0.0073 ml sap, and approximately 0.05 μc ^{137}Cs per ml sap (47 μc/mg fresh wt). If activity concentrations of the leaves upon which sap determinations were made are expressed on a fresh wt basis (19 μc/mg), it is seen that the ^{137}Cs concentrations in sap are about 2.6 times higher than for the entire leaf itself. Sap values should be considered only as approximations, since there is no estimation of the error involved in the determinations. However, they can be of significant value in assessing the organic turnover by sap-feeding insect populations. In subsequent discussion these values will be used to transform the turnover of radiocesium by aphids to consumption of sap both on a dry weight and volume basis.

Cesium-137 concentrations in the sessile canopy arthropods were determined from hand collections of species on individual leaves. In the more mobile insect groups, i.e., Diptera, flying Hymenoptera and Coleoptera, detectable levels of radiocesium were seldom found. This was due to mobility of these populations and the limited size of the experimental area. The levels of radioactivity in several of the more abundant arthropod species are given in Table II. Cesium-137 concentrations per gram are expressed as a per cent of the mean leaf concentrations (per gram) of the branches from which they were collected. Since, with a singular exception, there were no significant changes in body burden concentrations during the nine-week study period, the data are averaged for each month.

Highest ^{137}Cs levels were found in the leaf-eating herbivores — the tree cricket *Oecanthus* sp. and larvae of geometrid moths. The mean three-month summer concentration of ^{137}Cs in geometrids was 48.1% of the mean foliage concentration. Concentration factors in *Oecanthus* averaged 41.4% during June and July, but dropped off significantly in August for a grand mean of 28.8%. The low August values represent adults and probably result from their greater activity and immigration into the contaminated area from adjacent untagged trees. Sap-feeding herbivores such as aphids equilibrated at much lower ^{137}Cs levels than did the leaf-feeding species. Radioactivity levels in aphids averaged 6.0% of leaf values, which actually represented a factor of only 1.2% when compared to the ^{137}Cs concentrations in phloem sap. The Cicadellidae were another abundant group of sap-feeders with radiocesium concentrations not significantly different from aphids.

A specific predator of aphids is the aphidlion *Chrysopa* sp., a larval neuropteran of the family Chrysopidae. Aphidlions were relatively abundant during July and had average ^{137}Cs concentrations (6.2% of that in leaves) similar to their aphid food base. Larval and adult coccinellid predators of aphids also had ^{137}Cs levels similar to aphidlions. Cesium-137 body burdens of predaceous spiders averaged about 12% of leaf concentrations. The large variances associated with spider concentrations in all months suggest an important turnover and influx of uncontaminated individuals. Ballooning is a common means of dispersal for many canopy spiders and this mechanism could account for a dilution of the tagged populations by spiders from adjacent untagged trees. Two species of ants in the canopy, *Camponotus nearcticus* Emery and *Crematogaster lineolata* (Say), exhibited constant radiocesium levels throughout the three-month period. The average ant concentration of 20.6% was intermediate between cesium levels of predators and herbivores. Psocoptera concentrations were also intermediate.

These data (Table II) indicate a general decrease in ^{137}Cs content during movement along food chains with herbivorous insects (except for sap-feeders) having the highest concentrations, omnivores intermediate concentrations, and predators the lowest concentrations per unit weight. Canopy collections during the first summer after tagging showed ^{137}Cs concentration in herbivores

to be 0.36 of leaf concentrations. Predator concentrations averaged 0.70 that of their herbivore food base. The trophic efficiencies of radiocesium transfer were thus 36% and 82% for plant-to-herbivore and herbivore-to-predator, respectively. Crossley and Howden (1961) reported a similar decrease for ^{137}Cs concentrations in arthropod food chains in an herbaceous vegetation area. At present, however, radiocesium concentration by itself does not appear to be a reliable indicator of trophic position without previous knowledge of specific food chain relationships.

The initial movement of ^{137}Cs through arthropod communities after tagging exhibited a temporal lag between successive trophic levels, with peak radiocesium levels first occurring in vegetation, then herbivores, and finally predators. Similar distinctions in the rate of radiocesium movement through food chains can still be demonstrated when rapid changes in ^{137}Cs concentrations occur in a food base, i.e., the annual input of fresh litter to the forest floor with abrupt increases in radiocesium concentrations in the detritus base of decomposer populations.

3.3 FOLIAGE BIOMASS AND PRIMARY PRODUCTIVITY

Biomass estimates based upon litter fall offer the advantages of including total vegetational yield during the growing season, regardless of species composition or premature, senescent leaf drop. During the 1964 growing season, litter fall consisted of 143 g/m^2 of tagged *Liriodendron* leaves, 63 g/m^2 of non-tagged *Liriodendron* leaves, 18 g/m^2 of *Liriodendron* flowering parts, 98 g/m^2 of leaves from other deciduous species, predominantly understory, and 18 g/m^2 of pine needles (Olson and Waller 1965). Assuming that loss of tagged *Liriodendron* leaves from the forest plot due to wind action is balanced by the input of nontagged leaves from trees adjacent to the study plot, then total *Liriodendron* leaf biomass can be calculated to be 206 g/m^2 approximately 61% of the total vegetative production (exclusive of woody material). Using a mean oven-dry weight (105° C for 24 hrs) of 0.37 g/leaf, an average of 557 *Liriodendron* leaves per m^2 was calculated. Since the abundance of canopy arthropods was measured relative to densities per leaf, the total number of leaves per m^2 was used in converting arthropod biomasses to a m^2 basis.

The caloric content of *Liriodendron* leaves was 4.54 kcal/g dry weight (4.95 kcal/g ash free wt). An average value for conifer leaves (*Juniperus virginiana* L.) was 5.04 kcal/g dry wt. Using these values for approximations of the energy content of the various foliage elements we calculate a net annual foliage production by tree species to be 1.55×10^3 kcal/m^2. This figure is based upon a net green foliage production of 340 g/m^2 composed of 66% *Liriodendron* leaves and flowering parts, 29% foliage from other deciduous species, and 5% pine needles. Bray (1964) reported the net annual foliage

production by a sugar maple (*Acer saccharum* Marsh.) forest to be 1.57 × × 10^3 kcal/m^2 — quite similar to that reported here for the *Liriodendron* forest. Measured in this manner, the standing crop represents only the net primary foliage productivity of the system. Consumption of foliage by herbivores is not considered. Interpretation of ecosystem energetics also requires further consideration of the efficiencies of both primary and secondary productivity and their resultant energy expenditures of respiration.

3.4 LEAF AREA CONSUMED BY INSECTS

Estimation of foliage consumption was based upon a random sampling of *Liriodendron* leaves both between all of the major trees and within all levels of the canopy. Leaves for analysis were collected just before leaf drop and so provided an estimate for the entire growing season, with the exception of insect-induced senescent leaf fall during the summer months. Original leaf areas were measured with a polar planimeter, while a graph paper technique was used for the smaller areas consumed. The mean area of leaves sampled was 71.5 cm^2 (standard deviation of 31.7), with the random sampling procedure including leaves of a variety of different sizes. Insects were found to have consumed an average of 5.6% of total leaf area (standard deviation of 8.8), with some leaves having little damage and others considerable destruction due to insects (Fig. 5). There were no evidences of petiole consumption. Leaf damage due to leaf-mining insects was minimal, but these data have yet to be interpreted. The activities of foliage consumers and the resulting leaf damage did not affect the distribution of radiocesium within leaves (Fig. 5*B*) and, consequently did not bias estimation of ^{137}Cs concentrations in remaining leaf materials serving as future food bases. The localization of certain elements in scar tissue about wounds may present problems with the use of their radioisotopes in measuring food consumption.

The 5.6% consumption of *Liriodendron* leaves by herbivores in the canopy is in close agreement with values reported for other mesic, deciduous tree species. Bray (1964) found the percentage leaf utilization by primary consumers of *Acer* (maple), *Fagus* (beech), and *Fraxinus* (ash) to range between 5.0 and 7.7% in forests of southern Canada. With 61% (206 g/m^2) of the total tree foliage biomass in our experimental forest represented by *Liriodendron* leaves, 5.6% consumption by insects would raise the original production of foliage to 218 g/m^2 or 0.99 × 10^3 kcal/m^2. Assuming the same degree of leaf consumption for the remaining foliage elements would increase the total primary production estimate from 340 g/m^2 to 360 g/m^2 and from 1.55 × 10^3 kcal/m^2 to 1.64 × 10^3 kcal/m^2. A review by Bray (1964) has shown that the production of leaves by angiosperm forest trees is about 27% (23 to 30% range) of the total net above-ground production over the life

of the forest. If total foliage production in the *Liriodendron* forest was 27%, then total primary consumption attributable to leaf-feeders would be around 1.5% of the annual net primary production.

3.5 CANOPY ARTHROPOD BIOMASSES

Determinations of canopy arthropod biomasses were based upon measurements of population densities per leaf and extrapolated to a unit area basis using a conversion factor of 557 *Liriodendron* leaves/m^2. Density and mean species weight measurements were made weekly and averaged for each month (Table III). The observed biomass of omnivores was relatively low in comparison to that of herbivores and predators. The biomass of ants was probably underestimated considerably, since ants spent a major portion of their time on branches in movement between leaves and, consequently, were not adequately sampled with leaf assays. The biomass of Psocoptera averaged about 7.8 mg/m^2 for the summer, with populations increasing by an order of magnitude from June to August. Of the predators, spiders had unusually high average biomass (61 mg/m^2) with monthly values increasing from mid to late summer. The densities of other predators, i.e., Coccinellidae and Reduviidae, were low and spiders are probably the most important predatory group in the canopy. The numbers of leaf-feeding herbivores (geometrids and crickets *Oecanthus*) decreased progressively through the summer, but biomass increased due to the continued growth of individuals. The biomass represented by these two classes (74 mg/m^2) is only a partial estimate of the actual leaf-feeder biomass — early Spring weevil (*Odontopus calceatus* Say) damage and summer-long chrysomelid activity have been difficult to assess. The sap-feeders (Aphididae, Cicadellidae) constitute an equally important part of the total herbivore biomass. The biomass of aphids decreased abruptly from June to August, probably due to the effects of heavy predation. Reproduction continued, as evidenced by the reduction in average size. Leafhopper biomass, however, progressively increased despite a slight reduction in mean individual size. Since sap-feeders are typically sedentary forms and easily measured from leaf sampling, the total estimated biomass for sap-feeders (64 mg/m^2) is probably a more realistic value than that calculated for leaf-feeders.

These arthropod biomass data appear to be consistent with the leaf area consumption measurements reported above. Annual leaf production by *Liriodendron* was 218 g/m^2 with 5.6% or 12 g/m^2 consumed by insects. Averaged over an effective growing season from May to September (153 days) this amounts to a daily consumption of about 78 mg/m^2. Previous experience with lepidopteran larvae (*Thyridopteryx ephemeraeformis*) (Reichle and Dodson 1965), geometrids (present study), chrysomelid beetles *Chrysomela knabi* (Crossley 1966), and *Chrysochus auratus* (Fab.) (Williams and

Reichle 1968), has indicated that leaf consumption usually ranges from 50 to 150% of the dry body weight per day. Fluctuations within these limits vary between species and between different life history stages of the same insect. For mixed species populations of insects, Crossley and Howden (1961) and Crossley (1963a) have reported herbivores to consume between 108 and 136% of their dry body weight daily. Calculating from consumption rates (50–150%) and observed consumption (78 mg/m^2) gives a standing crop of canopy herbivores on *Liriodendron* between the limits of 40 and 120 mg/m^2. This range compares favorably with the combined biomass (74 mg/m^2) of the two major herbivores – tree crickets and caterpillars – although this range should be an over-estimate of standing crop since it would include biomass lost through mortality.

4. DISCUSSION

Geometrid larvae and the tree cricket *Oecanthus* are foliage-feeders in the canopy and together with chrysomelid beetles (not sampled) probably account for most of the herbivorous biomass. Aphids (*Macrosiphum liriodendroni*) and leafhoppers (Cicadellidae) are the major sap-feeders. Aphids form the base of several food chains. The aphidlion (*Chrysopa*) is a specific predator of aphids. Most of the coccinellids are predaceous, both as larvae and adults, and also feed chiefly upon aphids. Spiders are a ubiquitous group of predators, in the canopy and probably feed upon a variety of herbivore species. Although considered as a general group for practical purposes, the spider population was actually composed of five dominant genera: *Anyphaenella* (Anyphaenidae), *Misumenops* (Thomisidae), *Neoscona* (Araneidae), *Paraphidippus* (Salticidae), and *Spintharus* (Theridiidae). The ant *Crematogaster lineolata* tends aphids and collects their honeydew. *Crematogaster* has been observed transporting aphids between leaves in the canopy and in the vicinity of the sampling tower had seven aerial nests on branches of *Liriodendron*. The carpenter ant *Camponotus nearcticus* and the Psocoptera are best classified functionally as omnivores. In the canopy they are general scavengers feeding on fungi, fragments of dead insects, and similar materials.

Geometrid caterpillars constitute the largest herbivorous biomass in the forest canopy and, consequently, food consumption by this group would probably account for a large portion of the observed foliage consumption. The rate of foliage consumption can be calculated using the equation for estimating isotope intake ($I = kQ$). The biological half-life of ^{137}Cs in geometrids was 27 hrs at 15° C and 13 hrs at 24° C (Fig. 2). Corrected to mean field temperatures for June — August of 22.2° C, this gives a T_b of 14.3 hours and an elimination coefficient k, of 1.16 day^{-1}. The equilibrium levels of radiocesium in geometrids, Q, can be calculated from the mean individual

size and the mean ^{137}Cs concentration (6.08 mg × 22.6 pc/mg = 137.41 pc/individual). By substituting into the equation, radiocesium intake was determined to be 159.39 pc/day/individual. Since the ^{137}Cs level in the *Liriodendron* foliage food base was 47.0 pc/mg, this is equivalent to the consumption of 3.39 mg of foliage, or about 56% of the dry body weight consumed daily. Food intake by geometrid caterpillars thus falls at the lower limits of the consumption rates reported for most leaf-feeders. However, similar rates also have been found with larvae of the bagworm moth *Thyridopteryx ephemeraeformis* (Reichle, unpublished data).

The tree cricket *Oecanthus* is a foliage-feeder in the canopy during both its nymphal and adult life history stages. It is also possible to calculate the rate of food consumption by this species, if we estimate its biological half-life for radiocesium from the size-T_b relationship in Fig. 4. From the average fresh body weight of 28.15 mg, the biological half-life of *Oecanthus* should be approximately 10 hrs at 20° C or 8.5 hrs when corrected to mean environmental temperature of 22.2° C. The elimination coefficient, k, thus is 1.96 day^{-1}. Since we believe the ^{137}Cs concentrations in *Oecanthus* during August to have been diluted by immigration of untagged individuals, the mean June and July concentrations of 19.5 pc/mg are used as the equilibrium body levels. The radiocesium body burden Q is thus 176.28 pc (9.04 mg × × 19.5 pc/mg). Daily cesium intake becomes 345.51 pc for an average individual of 9.04 mg dry wt. *Oecanthus* averaged 7.35 mg dry wt of foliage consumed per day or about 81% of its body weight. The rate of food consumption by this species also falls into the general range typical of most herbivores (50 to 150% of body wt/day).

Based upon the individual rates of food consumption for tree crickets and geometrid caterpillars, it is possible to assess annual leaf intake by these populations and also the actual quantity of leaf biomass consumed in the canopy which can be attributed to their feeding activities. Geometrid larvae and *Oecanthus* consumed 56% and 81% of their body weight per day, respectively. Averaged over a 153 day growing season, these populations (standing crop taken from Table III) would consume 4.48 g/m^2 (geometrids) and 2.73 g/m^2 (*Oecanthus*) of the dry weight equivalence of foliage. In comparison to the 12 g/m^2 of foliage actually consumed, these two groups would account for 60% of leaf consumption by herbivores. Using the caloric equivalent of 4.54 kcal/g for *Liriodendron* foliage, energy flow for maintenance of these populations would be 20.34 $kcal/m^2$/year for geometrids and 12.39 $kcal/m^2$/year for *Oecanthus*.

Quite obviously, the feeding activities of sap-feeding insects can not be evaluated from observations and measurements of the leaves upon which they feed. Radioisotopic tracer methodology offers a tool which can be used to measure sap consumption by such species *in situ*. Radiocesium turnover by the aphid *Aphis fabae* was used to estimate sap intake by the forest species *Macrosiphum liriodendroni*. A biological half-life of 9 hrs (k = 1.85 day^{-1})

was used for the aphid. This value was obtained from the graph in Fig. 3 for bioelimination plus production of young and corrected by interpolation to mean canopy temperature. Since during most of the growing season the aphid population consists primarily of parthenogenetic females, the assumption is made that all individuals in the canopy were producing young. With a mean body size of 0.044 mg and a ^{137}Cs concentration of 2.8 pc/mg, average isotope intake was calculated at 0.028 pc/individual/day. Average ^{137}Cs concentrations in sap were a factor of five higher than leaves on a dry wt basis. With a mean leaf concentration of ^{137}Cs of 47.0 pc/mg dry wt, sap would be expected to average about 235 pc/mg dry wt. Daily isotope intake by aphids would then be equivalent to sap consumption of 2.2% (dry wt percentage sap/aphid). This is certainly an underestimation of aphid consumption. In their review of the biology of aphids, K e n n e d y and S t r o y a n (1959) cited Mittler's data for the willow-feeding aphid *Tuberolachnus salignus* (Gmelin) which gave 220% as the dry body wt consumed daily. However, Mittler found less than 5% nitrogen assimilation from fresh sap for adult specimens. If the uptake of radiocesium is correspondingly low, then our consumption estimate should be increased over 100%. Clearly, this is speculation at this time. Future experiments will be designed to evaluate the assimilation of radiocesium from sap by aphids, with eventual application to the measurement of food consumption by our forest populations.

Laboratory data on *Aphis fabae* showed the effects of the production of young on the turnover rate of radiocesium (Fig. 3). The elimination coefficients for aphids at 18° C were 0.792 day^{-1} (bioelimination only) and 1.189 day^{-1} (bioelimination plus production) — an increase of 0.397 day^{-1} or 39.7% per day due to the production of young. At 28° C the elimination coefficients were 1.848 day^{-1} (bioelimination only) and 2.373 day^{-1} (bioelimination plus production) — an increase of 0.525 day^{-1} or 52.5% per day due to the production of young. The production of young at 8° C was slight and had no effect upon radiocesium turnover. At 18° C and 28° C the production of young averaged 3.67 young/adult/day and 5.77 young/adult/day, respectively. Therefore, at 18° C the production of a single individual resulted in an increase in radiocesium turnover rate of 0.108 day^{-1} or 10.8%. At 28° C this increase was 0.091 day^{-1} or 9.1% per new individual. Within this 10° C span of temperature, the experimental aphid populations exhibited an acceleration in the turnover rate of radiocesium in the range of from 9.1% to 10.8% for the daily production of a single offspring by each member of the population. This technique would appear to offer a valuable means of estimating the production of young by natural populations of aphids and, possibly, other insects as well.

Liriodendron foliage production, corrected for insect consumption, was calculated to be 218 g/m^2 or about 61% of total leaf production in the study area. Extrapolating the herbivore biomass from *Liriodendron* to total foliage elements gives a value of 122 mg/m^2 for leaf-feeders. Assuming the 5.6% leaf

consumption value to hold for all tree species and using the same insect consumption limits (50 to 150% dry body wt consumed per day) yields a calculated range of leaf-feeder standing crop of 66 to 197 mg/m². Total measured herbivore biomass (including sap-feeders) was 138 mg/m² on *Liriodendron* leaves which becomes 227 mg/m² when related to complete canopy composition. Spider biomass was determined to be 61 mg/m² and 100 mg/m², respectively. Predaceous spider biomass thus constituted about 29% of the total measured standing crop of arthropods. Even if the upper range of calculated herbivore biomass (197 mg/m²) is used, spiders still represent about 24% of the foliage arthropod standing crop. This is about double the size of the predator population which would be expected to be supported by the existing herbivore biomass in comparison with reports from other habitats (M a c f a d y e n 1963). Insect populations living on branches may, in fact, comprise a substantial part of the spider prey. At the present it is not practicable to apply isotopic techniques for the estimation of food consumption by spiders. A difficulty arises in the uncertainty of specifying a definite food base and isotope input. Additional data are needed at this point on either the prey preferences or the diet composition of non-specific predators. Also lacking are T_b values for radiocesium in canopy spiders.

5. RADIOISOTOPE MODEL FOR SECONDARY PRODUCTION

The importance of predatory mortality upon secondary production by heterotrophic populations has long been recognized. The standing crop of herbivores in a given community represents neither the gross production of consumers nor the total biomass actually supported by that community. Likewise, plant consumption itself is seldom an accurate indication of the standing crop of primary consumers. Consequently, a concise interpretation of the energetics and secondary production in natural populations also requires study of the energy expenditures due to respiration as well as predatory and non-predatory mortality. Refinements in measurements of the metabolism of free-ranging organisms in the field are satisfying this first requirement. The employment of life table designs in population studies allows determination of species survirorship and non-predatory mortality. The ecologist, however, has yet to develop a realistic and practical method for measuring predatory mortality in natural populations irrespective of fluctuations in grazing pressure and prey biomass. Estimation of predatory mortality thus remains as an important factor in the calculation of secondary productivity.

The application of radioisotopes to the measurement of food consumption and energy flow in food chains involves the dynamic flux of tracer materials between and within trophic levels. The balance and loss concepts and transfer

kinetics vital to such an approach have led to the development of a preliminary model for the movement of radioisotopes through food chains (Crossley 1963b). In graphical form (Fig. 6) there are three basic trophic levels or compartments in the model — plant, herbivore, and primary predator. The energy and material flow between compartments occurs through consumption of vegetation and the feeding of predators upon herbivores. Predatory intake, in effect, is equivalent to the predatory mortality of herbivores. By using isotopic tracers, the standing crop of predator biomass can be used to estimate predatory mortality (grazing) of the preceeding (herbivore) compartment.

Productivity cannot be interpreted separately from other phenomena of the food chain. Standing crops, rates of feeding, total energy intake, and energy utilization for maintenance are all variables which ultimately affect productivity. Radioactive tracers are among the newer tools which are being used to measure phenomena associated with food chains. When animals feed upon plants containing certain radioisotopes a steady-state condition is attained. At equilibrium concentrations the daily intake of radioisotope is balanced by daily elimination. In the food chain model (Fig. 6) intake is through feeding alone, while there are three principal pathways of elimination or loss: (1) egestion, which encompasses bioelimination and non-assimilated isotope, (2) non-predatory mortality, and (3) predatory mortality. If mortality is excluded (as in short-term field or laboratory experiments), radioisotope input to either of the animal compartments can be predicted from egestion measurements and compartmental concentrations of radioisotope. Under field conditions the losses due to mortality may result in a reduction in size and radioisotope content of the herbivore or predator compartment. If mortality is balanced by production, however, the compartment size is maintained.

Predatory mortality of the predator compartment is usually an order of magnitude lower than for the herbivore compartment and can be minimized for first order approximations. Allowances for non-predatory mortality remain essential; however, the importance of non-predatory mortality is not peculiar to the model itself, but an inherent variable in any approach to secondary productivity. Data currrently are becoming available with which to apply this radioisotopic model for quantifying food chain phenomena and estimating secondary productivity. One of us (Crossley) is currently applying the model to herbaceous insect communities living in an area contaminated with radioactive wastes (Crossley and Howden 1961). When sufficient supporting data become available, we plan to also analyze secondary production in the *Liriodendron* canopy insect community and the cryptozoan community of the same forest floor (Reichle and Crossley 1965). The results of these studies will be reported separately.

We are indebted to Mr. Russell M. Norton, now at the University of Kentucky, for his assistance in sampling the canopy arthropod populations. Field and laboratory assistance by Mrs. Gladys J. Dodson and Mr. Marvin H. Shanks is gratefully acknowledged. Our colleagues,

Dr. J. S. Olson and Mr. Hubert D. Waller, generously permitted access to unpublished data arising from their botanical investigations in the radiocesium-tagged *Liriodendron* forest stand. Identifications of spiders and ants were provided by Mr. Bennett Moulder and Dr. A. C. Cole, respectively, both of the University of Tennessee.

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Table I

Weekly ^{137}Cs concentrations in *Liriodendron* leaves on branches sampled during the study period. Cesium values are pc per mg dry weight

Date of collection	No. of leaves examined	$\bar{x}$ branch concentration
June 18	83	42.3
June 23	88	43.3
June 29	73	49.5
July 6	96	43.7
July 14	81	50.6
July 28	70	32.9
August 3	95	56.4
August 13	83	46.0
August 16	86	58.4
Mean	84	47.0 ± 2.59

Table II

Cesium-137 concentrations in canopy arthropods expressed as a percentage of leaf concentrations. Monthly values are means of three collections; $\bar{x}$ = mean, *SD* = one standard deviation. Grand means are calculated from original weekly collections

Trophic position		Herbivore				Omnivore		Predator		
		leaf-feeder		sap-feeder						
month		*Geometridae*	*Oecanthus*	*Macrosiphum*	*Cicadellidae*	*Formicidae*	*Psocoptera*	*Araneida*	*Chrysopa*	*Coccinellida*
June	$\bar{x}$	40.6	34.3	5.1	—	21.4	10.0	13.6	—	4.0
	SD	22.86	4.32	1.63	—	1.51	—	9.90	—	0.86
July	$\bar{x}$	58.1	48.5	5.3	5.1	20.1	12.6	10.7	6.2	7.4
	SD	—	12.68	1.87	1.86	1.43	6.43	12.01	1.01	—
August	$\bar{x}$	49.7	12.1	9.8	7.9	19.7	—	11.3	—	8.2
	SD	4.60	6.22	—	—	—	—	9.19	—	—
Grand	$\bar{x}$	48.1	28.8	6.0	6.0	10.6	12.2	11.9	6.2	5.9
	SD	12.52	17.93	2.36	2.10	1.28	5.95	9.13	1.01	2.28

Table III

Population density and biomass estimates of the dominant canopy arthropods on *Liriodendron tulipifera* June through August 1965. Data are based upon weekly samples of vegetation with arthropod densities per leaf converted to m^2 basis using 557 *Liriodendron* leaves/m^2

Trophic position	Herbivore				Omnivore		Predator	
	leaf-feeder		sap-feeder					
month	*Geometridae*	*Oecanthus*	*Macrosiphum*	*Cicadellidae*	*Formicidae*	*Psocoptera*	*Araneida*	Total mg/m^2
June								
$\bar{x}$ mg wt	3.77	2.89	0.058	2.26	0.65	0.25	2.94	
No./m^2	13.47	4.11	1248.42	6.08	2.51	7.01	6.71	
mg/m^2	50.82	11.87	72.78	13.75	1.64	1.79	19.73	172.38
July								
$\bar{x}$ mg wt	5.30	10.51	0.043	2.22	0.92	0.23	2.59	
No./m^2	8.16	3.59	221.92	15.12	1.19	20.18	38.07	
mg/m^2	43.24	37.69	9.48	33.52	1.09	4.68	98.70	228.40
August								
$\bar{x}$ mg wt	9.17	13.73	0.031	2.05	0.60	0.24	2.14	
No./m^2	6.86	1.20	209.05	26.98	0.75	71.35	30.36	
mg/m^2	62.94	16.48	6.48	55.31	0.45	16.90	65.02	223.58
$\bar{X}$ mg/m^2	52.33	22.01	29.58	34.19	1.06	7.79	61.15	208.11

Fig. 1. Lift truck with 65-ft (20-meter) boom used in sampling canopy vegetation (background shows ^{137}Cs tagged *Liriodendron tulipifera* forest in July aspect)

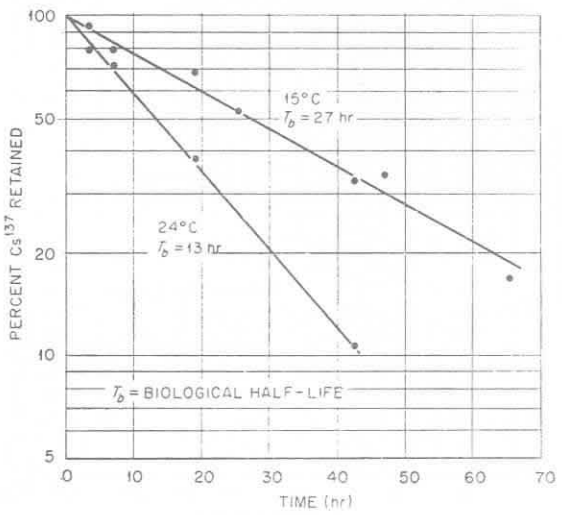
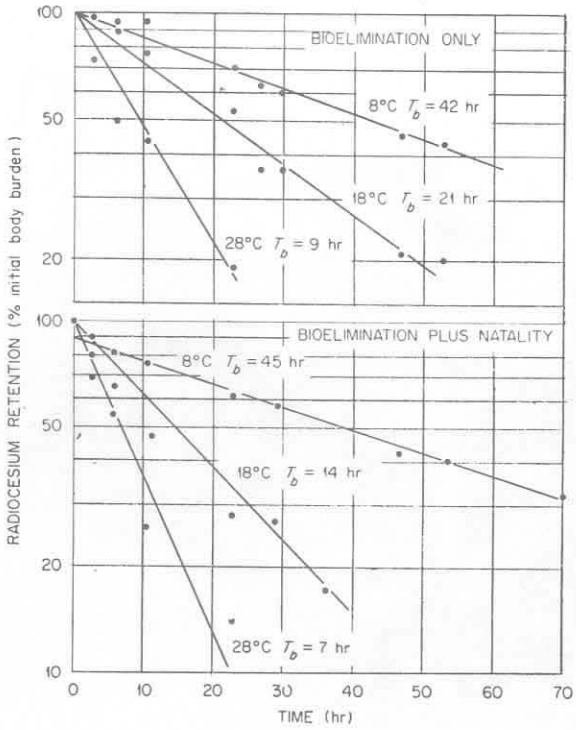


Fig. 2. The influence of temperature upon radiocesium retention by geometrid caterpillars
Biological half-lives follow a Q_{10} of approximately 2, with a doubling of the elimination rate of ^{137}Cs over a 10°C temperature increase


BIOELIMINATION ONLY
8°C T_b = 42 hr
18°C T_b = 21 hr
28°C T_b = 9 hr
BIOELIMINATION PLUS NATALITY
8°C T_b = 45 hr
18°C T_b = 14 hr
28°C T_b = 7 hr
RADIOCESIUM RETENTION (% initial body burden)
TIME (hr)

Fg. 3. Interactions of temperature and the production of young on radiocesium retention by the bean aphid *Aphis fabae*

Top, bioelimination by mothers and young; bottom, bioelimination plus natality. Natality induces a significant increase in the turnover rate of ^{137}Cs except at 8°C where young production is minimal. Radiocesium retention shows a temperature Q_{10} of approximately 2

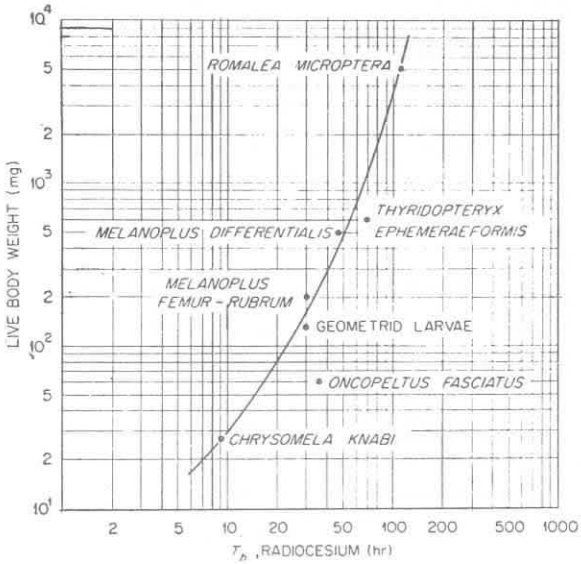


Fig. 4. Relationship between body size and radiocesium biological half-lives of herbivorous insects:

grasshoppers *Romalea microptera* (Beauvais), *Melanoplus differentialis* (Thomas), and *Melanoplus femur-rubrum* (DeGeer); lepidopteran larvae *Thyridopteryx ephemeraeformis* (Haworth) and *Geometridae*; milkweed bug *Oncopeltus fasciatus* (Dallas); and the leaf beetle *Chrysomela knabi* Brown

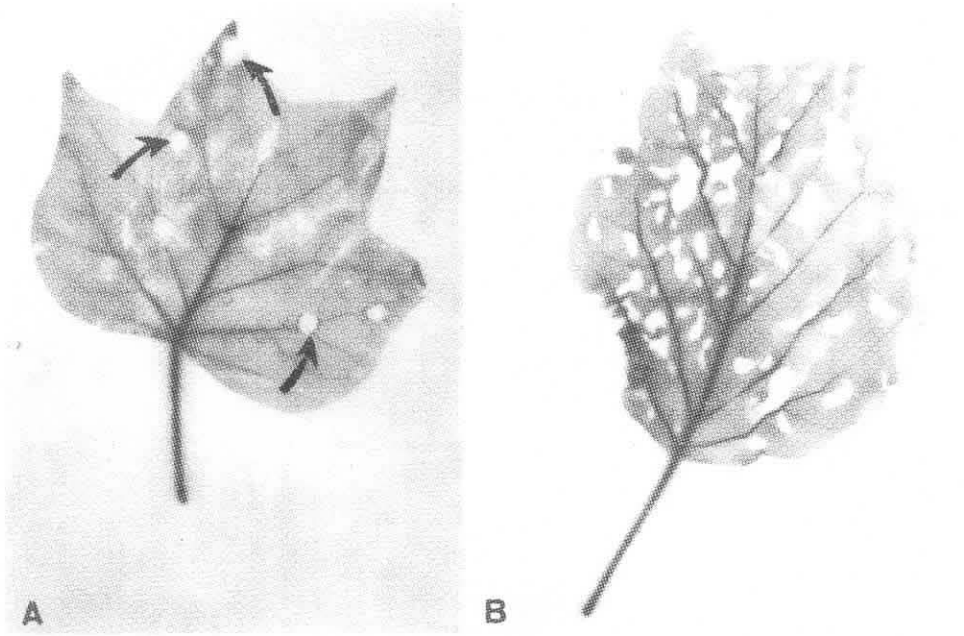


Fig. 5. Audioradiograms of *Liriodendron tulipifera* leaves showing the relative distribution of ^{137}Cs

A — leaf with minor insect consumption and leaf punches (arrows) removed for radioanalysis. *B* — leaf exhibiting heavy insect consumption

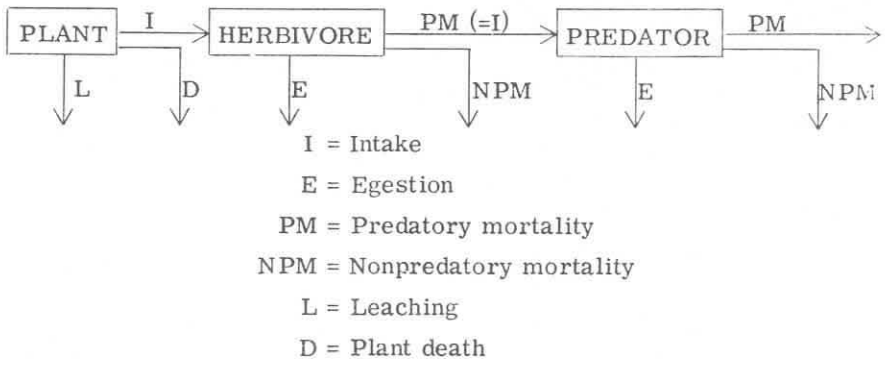


Fig. 6. Model of the distribution and exchange of radiocesium between the trophic compartments of an herbivorous food chain

At steady-state conditions, determination of the loss parameters allows quantification of the intake terms. Predatory intake is, in effect, equivalent to non-predatory mortality of herbivores. Standing crop of a compartment plus mortality represents the gross production by that trophic level